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Genetic parameters for docility, weaning weight, yearling weight, and intramuscular fat percentage in Hereford cattle¹

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ABSTRACT: Cattle behavior, including measures of docility, is important to beef cattle producers not only from a human safety perspective but also due to potential correlations to economically relevant traits. Field data from the American Hereford Association was used to estimate genetic parameters for chute score (CS; $n = 25,037$), weaning weight (WW; $n = 24,908$), yearling weight (YW; $n = 23,978$), and intramuscular fat percentage (IMF; $n = 12,566$). Single-trait and bivariate animal models were used to estimate heritabilities and genetic correlations. All models included fixed effects of sex and contemporary group, defined as herd–year–season, and direct genetic and residual components were included as random effects. For CS and WW, additional random effects of maternal genetic and maternal permanent environment were also fitted. For CS, WW, YW, and

IMF, heritability estimates were 0.27 ± 0.02 , 0.35 ± 0.03 , 0.36 ± 0.02 , and 0.27 ± 0.02 , respectively. Genetic correlations between CS and WW, CS and YW, CS and IMF, WW and YW, WW and IMF, and YW and IMF were -0.12 ± 0.06 , -0.10 ± 0.05 , -0.08 ± 0.06 , 0.47 ± 0.05 , -0.19 ± 0.09 , and -0.41 ± 0.05 , respectively. Heritability estimates for all traits suggest that they would respond favorably to selection and that selection for increased WW or YW could decrease marbling. Genetic correlations between CS and WW, YW, and IMF were all favorable but weak, suggesting that selection for improved docility will not have negative consequences on growth or carcass quality. Furthermore, maternal additive and maternal permanent environmental variances for CS were near 0, suggesting that their inclusion in National Cattle Evaluations is not warranted.

Key words: beef cattle, docility, genetic parameters, intramuscular fat percentage.

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INTRODUCTION

It is well documented that cattle vary in their response to stressors and environmental changes. In fact, overly aggressive animals are considered undesirable, given the potential safety risks to human

handlers (Cafe et al., 2011a; Turner et al., 2011). Conversely, calm temperament has been associated with increased ADG, health, and meat quality and superior responses to infections, which improves overall herd productivity (Burrow, 1997; Fell et al., 1999; Kadel et al., 2006). Moreover, temperament traits are important because feedlot managers and producers would suggest that excitable cattle could be more costly to raise in terms of required handling time, labor, and equipment repair (Hall et al., 2011). Due to the associations between temperament and production traits, assessment of beef cattle temperament has increased in recent years (Norris et al., 2014). Consequently, several breed associations are now routinely measuring docility to include in national cattle evaluations (Beckman et al., 2007; Norris et al., 2014). The phenotype that is currently used in national cattle evaluations is the subjective measure of chute score (Beef Improvement Federation, 2010).

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Despite the attention that quantifying temperament has received, there is not a general consensus relative to the genetic correlations between docility and economically relevant traits, because these results could vary due to several different factors (e.g., method of evaluating docility, rearing conditions, breeds, etc.; Haskell et al., 2014; Norris et al., 2014). Before a docility selection metric can be added to a genetic evaluation, any potential antagonisms with economically relevant traits or indicator traits should be quantified. Consequently, the objective of the current study was to estimate genetic parameters for chute score, weaning weight, yearling weight, and intramuscular fat percentage in Hereford cattle.

MATERIALS AND METHODS

Animal Care

Data were provided by the American Hereford Association (AHA) and, therefore, the project was not subject to animal care and use committee approval.

Data

Initial data from 130,263 animals, born between 1979 and 2014, were supplied by the AHA (Kansas City, MO). Animal records included 205-d weight adjusted for calf and dam age (weaning weight [WW]), age-adjusted yearling weight (YW), chute score (CS), and age-adjusted intramuscular fat percentage (IMF) measured via ultrasound following Beef Improvement Federation guidelines (Beef Improvement Federation, 2010). Data were edited such that animals without sire or dam information were removed. For CS, contemporary groups (CG) of less than 10 animals or without variation in CS scores were removed. For YW, animals from CG with less than 10 animals were removed. For IMF, records from CG with less than 10 animals were considered as missing values. Records from 25,037 animals weaned between 2010 and 2014, with YW from 2011 and 2015, were used. The final pedigree file included 172,867 animals, with 9,079 sires and 62,272 dams.

Chute scores were obtained at weaning, following the method proposed by Grandin (1993) and following the scoring system recommended by the *Guidelines for Uniform Beef Improvement Programs* (Beef Improvement Federation, 2010) in which high scores reflect poor docility. According to this classification, animals with scores of 1 are considered docile or calm, a score of 2 indicates animals that are restless or shifting, a score of 3 indicates animals that are squirming or nervous, a score of 4 indicates animals that are flighty (wild), and scores of 5 and 6 represent aggressive and very aggressive animals, respectively (Grandin, 1993;

Table 1. Descriptive statistics for chute score a weaning weight, yearling weight, and intramuscular fat percentage

Trait	No.	Mean	Min ¹	Max ²	SD	CV, %
Chute score	25,037	1.22	1	6	0.53	43.2
Weaning weight, kg	24,908	264.6	85.4	469.7	42.5	16.1
Yearling weight, kg	23,978	414.1	147.7	743.9	80.4	19.4
Intramuscular fat, %	12,556	3.2	0.6	9.6	1.0	32.6

¹Min = the minimum value.

²Max = the maximum value.

Beef Improvement Federation, 2010). The final data file included 25,037 records for CS, 24,908 records for WW, 23,978 records for YW, and 12,566 records for IMF. The descriptive information of WW, YW, CS, and IMF are presented in Table 1. Chute score was characterized by a skewed distribution as a consequence of a greater number of observations for score 1 ($n = 20,495$; representing 81.86% of the total observations) compared with score 2 ($n = 3,646$), score 3 ($n = 728$), score 4 ($n = 143$), score 5 ($n = 23$), and score 6 ($n = 2$).

For each trait, 2 weaning seasons were defined: January through June and July through December. Contemporary groups for each trait were formed by the combination of herd–year–season.

Statistical Analyses

In the current study, CS was treated as a linear trait. Six bivariate linear–linear animal models were fitted to estimate (co) variance components between traits, and starting values for each trait were initially estimated with similar single-trait animal models using ASReml software (Gilmour et al., 2009). Final models included the fixed effects of sex and CG. Direct additive genetic and residual effects were included as random effects. For CS and WW, maternal genetic and maternal permanent environmental components were also fitted as random effects.

In matrix notation, the model for YW and IMF can be represented as

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}. \quad [1]$$

When CS and WW were analyzed, the model can be represented as

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{p} + \mathbf{e}, \quad [2]$$

in which \mathbf{Y} represents the vector of records for the traits; \mathbf{b} is the vector of fixed effects; \mathbf{a} is the vector of random additive genetic effects of the animals; \mathbf{m} is the vector of random maternal genetic effects of the dams; \mathbf{p} is the vector of maternal permanent environment effects of the dams; \mathbf{e} is an unknown vector of random

environmental effects; and \mathbf{X} , \mathbf{Z} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 are incidence matrices relating observations to fixed, animal (model 1), animal, maternal, and maternal permanent environmental effects (model 2), respectively.

For model 2, the expectations and (co) variance matrices for random effects are described as

$$\mathbf{E} \begin{bmatrix} \mathbf{Y} \\ \mathbf{a} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}$$

$$\mathbf{V} \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_a & \mathbf{G}_{am} & \mathbf{0} & \mathbf{0} \\ \mathbf{G}_{am} & \mathbf{G}_m & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix} =$$

$$\begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_a & \mathbf{A} \otimes \mathbf{G}_{am} & \mathbf{0} & \mathbf{0} \\ \mathbf{A} \otimes \mathbf{G}_{am} & \mathbf{A} \otimes \mathbf{G}_m & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_D \otimes \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_O \otimes \mathbf{R} \end{bmatrix},$$

in which \mathbf{G}_a , \mathbf{G}_m , \mathbf{P} , and \mathbf{R} denote the matrices containing additive genetic, maternal genetic, maternal permanent environmental, and residual (co) variance components, respectively; \mathbf{G}_{am} represents the direct-maternal additive genetic covariance; \mathbf{A} is the numerator relationship matrix; \mathbf{I}_D is an identity matrix accounting for the number of dams with offspring; and \mathbf{I}_O is an identity matrix for the total number of observations.

RESULTS AND DISCUSSION

Heritability estimates using single-trait models are presented in Table 2. Direct heritability estimates were 0.36 ± 0.02 , 0.35 ± 0.03 , 0.27 ± 0.02 , and 0.27 ± 0.02 for YW, WW, CS, and IMF, respectively. (Co) variance estimates can be found in Table 3 and heritability, genetic, and residual correlation estimates can be found in Table 4. For CS, all bivariate models included only direct effects as maternal components estimated from the univariate analysis were near 0.

Norris et al. (2014) stated that among all methods documented to assess temperament or docility in cattle, the most common methods used are CS, pen score, and exit velocity. Regardless of the method used to measure docility, direct heritability estimates in the literature have a considerable range (from 0.03 to 0.67; Fordyce et al., 1982; Hearnshaw and Morris, 1984; Haskell et al., 2014). The direct heritability estimate of 0.27 (0.02) reported from the current study is similar to the range of estimates (0.29 to 0.34) reported by Beckman et al. (2007), who

Table 2. Variance component and heritability estimates (SE) using single-trait models for chute score, weaning weight, yearling weight, and intramuscular fat percentage

Parameter ¹	Chute score	Weaning weight, kg	Yearling weight, kg	Intramuscular fat, %
σ_a^2	0.056 (0.004)	327.9 (29.5)	2,076.2 (127.0)	0.26 (0.02)
σ_m^2	0.000 (0.000)	141.1 (21.8)	—	—
σ_{a-m}	0.000 (0.000)	-124.5 (22.0)	—	—
C^2	0.008 (0.002)	130.8 (12.8)	—	—
σ_e^2	0.145 (0.003)	449.5 (17.9)	3,685.9 (97.6)	0.72 (0.02)
σ_p^2	0.208 (0.002)	924.7 (10.4)	5,762.1 (62.2)	0.98 (0.01)
h_a^2	0.27 (0.02)	0.35 (0.03)	0.36 (0.02)	0.27 (0.02)
h_m^2	0.00 (0.00)	0.15 (0.02)	—	—
r_{am}	0.00 (0.00)	-0.58 (0.06)	—	—

¹ σ_a^2 = additive genetic variance; σ_m^2 = maternal genetic variance; σ_{a-m} = direct-maternal genetic covariance; C^2 = maternal permanent environmental variance; σ_e^2 = residual variance; σ_p^2 = phenotypic variance; h_a^2 = direct heritability; h_m^2 = maternal heritability; r_{am} = direct-maternal correlation.

used a univariate linear animal model using standardized scores instead of raw CS. Flight speed (FS), the velocity at which the animal leaves a restraining device, has been studied by several authors (e.g., Burrow, 1997; Haskell et al., 2014). The CS heritability estimate estimated herein (0.27 ± 0.02), using a single-trait animal model, was similar to the estimate of 0.28 (0.05) for FS reported by Sant'Anna et al. (2015). Hoppe et al. (2010) estimated genetic correlations between CS and FS ranging between 0.57 and 0.98 in different beef cattle breeds, and more recently, Sant'Anna et al. (2013) reported strong genetic correlation estimates between temperament score, crush score, and FS, ranging from 0.76 to 0.99. Both studies suggest that a large portion of the genes underlying one measure of docility also underlie other measures of docility. Similarly, results from Kadel et al. (2006) suggest that the ranking of animals based on genetic predisposition for temperament is consistent over time. These authors reported genetic correlations ranging from 0.98 and 0.96 for flight time and crush score measured over time. To the contrary, disagreements between measures of docility have been reported and are largely confined to differences between objective and subjective measures of FS. For example, Burrow and Corbet (2000) reported moderate (0.45) genetic correlations and low (0.02) phenotypic correlations between the subjective and objective measures of FS scores, suggesting that the observers of FS could not adequately differentiate animals using a 1 to 5 scale to report FS. This could be due to preconceived bias or the inability to discriminate scores, particularly those that are intermediate. However, the same authors reported genetic and phenotypic correlations between objective FS and subjective crush score of -0.45 and -0.44, respectively, suggesting that relative to subjective measurements of temperament, crush score is more desirable than a subjective measure of FS.

Table 3. (Co) variance component estimates (SE) using 2-trait models for chute score, weaning weight, yearling weight, and intramuscular fat percentage

Parameter ¹	Trait 1–Trait 2 ²					
	CS–WW	CS–YW	CS–IMF	YW–WW	IMF–WW	YW–IMF
$\sigma^2_{a,1}$	0.061 (0.004)	0.060 (0.004)	0.054 (0.005)	2,017.4 (121.2)	0.26 (0.02)	1,413.2 (123.1)
$\sigma^2_{e,1}$	0.149 (0.003)	0.149 (0.003)	0.131 (0.004)	3,733.5 (94.1)	0.71 (0.02)	2,938.9 (98.5)
$\sigma^2_{a,2}$	326.8 (29.4)	2,073.5 (126.9)	0.26 (0.02)	293.0 (26.9)	183.3 (26.6)	0.26 (0.02)
$\sigma_{a-m,2}$	–123.3 (21.9)	–	–	–84.8 (18.6)	–63.2 (21.5)	–
$\sigma^2_{m,2}$	140.1 (21.7)	–	–	140.7 (18.7)	99.1 (23.4)	–
$\sigma^2_{e,2}$	450.6 (17.9)	3,687.8 (97.6)	0.72 (0.02)	479.1 (16.8)	475.0 (18.7)	0.72 (0.02)
$C^2_{e,2}$	130.0 (12.7)	–	–	98.6 (10.6)	107.0 (16.0)	–

¹ σ^2_a = additive genetic variance; σ^2_m = maternal genetic variance; σ_{a-m} = direct-maternal genetic covariance; C^2 = maternal permanent environmental variance; σ^2_e = residual variance; σ^2_p = phenotypic variance. Parameter 1 and parameter 2 relate to trait 1 and 2, respectively.

²CS = chute score; WW = weaning weight (kg); YW = yearling weight (kg); IMF = intramuscular fat percentage.

Among U.S. beef cattle breed associations that provide a selection tool to improve docility, some breed associations suggest scoring docility at yearling age and others at weaning. The benefit of scoring docility at weaning is the ability to garner CS information on more animals (larger CG) before selection for other traits (e.g., growth) occurs. However, for any trait measured at weaning, there is the potential that both maternal genetic and maternal permanent environmental effects could play a substantial role in explaining the phenotypic variation of the trait. In the current study, estimates of both maternal genetic and maternal permanent environmental components for CS were near 0. This is in agreement with the results from several other authors suggesting that the maternal components for docility are low (Burrow, 2001; Prayaga and Henshall, 2005; Beckman et al., 2007) and that the inclusion of these effects in genetic evaluations for CS is not warranted.

In the current study, direct heritability estimates for WW ranged from 0.23 to 0.35, with smaller maternal heritability estimates ranging from 0.12 to 0.15. The direct heritability estimates for WW with CS and WW with YW followed the same pattern as the estimates using a single-trait model (0.35 ± 0.03 and 0.32 ± 0.03 , respectively); however, the estimate for WW with IMF was lower (0.23 ± 0.03). A similar pattern was observed for maternal heritability estimates for WW with CS and WW with YW (0.15 ± 0.02) and for WW with IMF (0.12 ± 0.03). The lower heritability (direct and maternal) estimates for WW when fitted in a bivariate model with IMF are due to the fact that a reduced subset of animals was used such that all animals had both traits recorded. This was done because a comparatively large number of WW CG did not have IMF observations. The direct heritability estimates were within the range of literature values, 0.07 to 0.57, reported by other authors (Schoeman and Jordaan, 1999; Plasse et al., 2002). Maternal heritability estimates for WW in the literature vary from 0.06 to 0.21 (Haile-Mariam and Kassa-Mersa, 1995; Diop and Van

Vleck, 1998). The maternal heritability estimates for WW from the current study (0.15 ± 0.02) were slightly lower than the weighted mean of 0.18 published by Koots et al. (1994). In the current study, a negative and significantly different from 0 direct-maternal covariance was estimated for WW. Both positive and negative estimates have been reported in the literature; however, the majority of estimates tend to be negative (Meyer, 1992; Schoeman and Jordaan, 1999; Speidel et al., 2007). Heritability estimates for YW ranged from 0.35 to 0.36 with small SE (from 0.02 to 0.03), within the range of estimated values in different beef cattle populations (e.g., Meyer, 1992; Mohiuddin, 1993).

Using 2-trait animal models, the heritability estimate for IMF was identical (0.27 ± 0.02) to the estimate using a single-trait model. The direct heritability for IMF estimate in this study was similar to the estimate from MacNeil et al. (2010) using Angus field data (0.31 ± 0.03) and to the estimates of 0.18, 0.30, and 0.25 for bulls, heifers, and steers, respectively, previously reported by MacNeil and Northcutt (2008). The estimate from the current study is slightly lower than the estimate of 0.41 reported by Bertrand et al. (2001) and the more recent estimate of 0.38 reported by Mateescu et al. (2015) in Angus cattle.

Estimates of genetic and environmental correlations among traits are presented in Table 4. Only the genetic correlation between YW and WW was moderate and positive. The rest of the genetic correlation estimates were negative, with a range from -0.41 to -0.08 . The negative genetic correlation estimate between YW and IMF was the strongest (-0.41 ± 0.05) followed by IMF with WW (-0.19 ± 0.09). The lowest genetic correlation estimates in magnitude were between CS and WW, CS and YW, and CS and IMF, with values of -0.12 ± 0.06 , -0.10 ± 0.05 , and -0.08 ± 0.06 , respectively. The highest residual correlations were between YW and WW (0.31 ± 0.02) and between YW and IMF (-0.48 ± 0.02). Residual correlations

Table 4. Estimates of heritabilities (on diagonal), genetic correlations (above diagonal), and environment correlations (below diagonal) with their SE from bivariate models for chute score, weaning weight, yearling weight, and intramuscular fat percentage

Trait ¹	CS	WW _d	WW _m	YW	IMF
CS	0.29 (0.02)	-0.12 (0.06)	0.02 (0.07)	-0.10 (0.05)	-0.08 (0.06)
WW _d	-0.04 (0.02)	0.23 to 0.35 (0.03)	-0.58 to -0.47 (0.06 to 0.11)	0.47 (0.05)	-0.19 (0.09)
WW _m	-	-	0.12 to 0.15 (0.02 to 0.03)	0.46 (0.06)	0.23 (0.10)
YW	-0.04 (0.02)	0.31 (0.02)	-	0.35 to 0.36 (0.02 to 0.03)	-0.41 (0.05)
IMF	0.02 (0.02)	0.05 (0.02)	-	-0.48 (0.02)	0.27 (0.02)

¹CS = chute score; WW_d = direct genetic component for weaning weight; WW_m = maternal genetic component for weaning weight; YW = yearling weight; IMF = intramuscular fat percentage.

among all the other traits were close to 0, with a range from -0.04 to 0.05, with relatively large SE of 0.02.

The positive genetic correlation between WW and YW is in agreement with other published estimates (Koots and Gibson, 1996). Of specific interest in the current study were the genetic correlations between CS and WW, YW, and IMF. The genetic correlation between CS and WW was low and negative -0.12 ± 0.06 , indicating that selection for higher WW would result in selecting animals with calmer temperament. Similar genetic correlations have been reported by Sant'Anna et al. (2013) for WW and FS, WW and temperament score, WW and crush score, and WW and movement score of -0.08 ± 0.07 , -0.19 ± 0.07 , -0.15 ± 0.09 and -0.01 ± 0.08 , respectively. Figueiredo et al. (2009) reported positive and favorable genetic correlations (0.36) between flight distance score and WW in Nellore cattle, where 1 refers to very reactive animals and 5 refers to very docile animals. These authors agree that selection for docile animals should manifest in modest improvements in WW. However, Burrow (2001) did not find genetic associations between WW and FS score (genetic correlation) [r_g] = 0.00) or between YW and FS score (r_g = 0.01) in a tropically adapted composite breed of cattle. In agreement with Burrow (2001), Prayaga and Henshall (2005) did not find significant genetic correlations between flight times and WW or YW in tropical beef cattle populations. Additionally, Phocas et al. (2006) estimated genetic correlations close to 0 between YW and docility score (0.08 ± 0.09) in Limousin heifers.

Results suggest the existence of low and favorable genetic correlations between temperament and WW or YW, suggesting that individuals with more desirable temperament could have slightly improved performance (Figueiredo et al., 2009; Hoppe et al., 2010; Sant'Anna

et al., 2012). The underlying physiological explanation for these associations is not well documented in intensive systems (Sant'Anna et al., 2015). Plasma cortisol and other metabolite concentrations, mainly glucose and lactate, have been significantly associated with poor temperament (Cafe et al., 2011b). Cafe et al. (2011b) suggested that more excitable animals show greater activation of the hypothalamic–pituitary–adrenal axis resulting in the production of more cortisol and glucose, and several authors have found that lower levels of cortisol are associated with higher growth rates (Purchas et al., 1980).

Few authors have quantified the potential genetic relationship between docility and IMF as a measure of meat quality. The genetic correlation between IMF and CS from the current study (-0.08 ± 0.06) was similar to that observed by Reverter et al. (2003), who estimated a negative and close to 0 genetic correlation between IMF and flight time (-0.05) in tropically adapted cattle breeds. Results from Kadel et al. (2006) suggested that improved temperament, evaluated using crush score and FS, was genetically correlated with improved tenderness in tropically adapted breeds of beef cattle. Shear force, a measure of tenderness, has been genetically associated with temperament by several authors, with the general consensus that more excitable cattle are prone to produce tougher beef and a higher incidence of dark cutters (Voisin et al., 1997; King et al., 2006; Hall et al., 2011). Although the influence of IMF on beef palatability has been controversial, the visual appearance due to marbling is often associated with favorable meat quality and certainly plays an important role in purchasing decisions and price (Chambaz et al., 2003). The results from the current study suggest that marbling should not be negatively impacted by long-term selection for CS and could be slightly improved. Admittedly, the genetic correlations estimated herein are confined to a population whereby the majority of cattle were considered to be calm. In populations where a greater proportion of animals were considered aggressive, the genetic correlations between CS and IMF could be greater.

In conclusion, heritability estimates from the current study suggest that CS would respond favorably to selection and improvement in this trait could be made. For CS, the maternal component did not explain any of the phenotypic variation, suggesting that inclusion of a maternal effects model is not warranted for CS. Although favorable associations were found between docility and WW, YW, and IMF, the SE were relatively large.

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